

CHROMOSOMES OF MEXICAN *SEDUM* IV. HETEROPLOIDY IN *SEDUM MORANENSE*

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ABSTRACT

At least 18 different chromosome numbers, from $n = 21$ to $n = 153$ are reported for 51 collections of *Sedum moranense* from 45 localities, most of them in east central Mexico. At least ten levels of ploidy, up to 16-ploid, are represented, mostly based on $x = 18-21$, including probable 5-, 7-, and 9-ploids. Dysploid variants occur at several levels of ploidy, and some other plants have extra chromosomes of standard size; at least six have B-chromosomes. In most collections the bivalents do not differ greatly among themselves in size, but four collections from the Sierra de Guanajuato have strongly asymmetrical karyotypes and also anomalous chromosome numbers ($n = 52, 54$). In spite of the great variation in their chromosomes, most collections are very similar in their morphology, and, except for the larger flowers of the 14-ploid subspecies *grandiflorum*, no correlation is apparent between morphology and chromosome number.

This paper is the fourth in a series reporting the chromosomes of 100 or so species of Mexican *Sedum*. A general introduction, materials and methods, and acknowledgments are given in the first paper (Uhl, 1976). *Sedum moranense* is singled out for special attention here because it has the greatest cytological diversity of all the Mexican Crassulaceae, which as a group are distinguished for the great variety in their chromosomes.

The Mexican Crassulaceae have an exceptionally broad array of chromosome numbers (heteroploidy), from $n = 7$ to $n = \text{ca. } 320$ (Uhl, 1972-1980). Polyploidy is common, ranging to at least 20-ploid, and very extensive dysploidy also occurs in some genera and in some groups of related species. In some cases a very broad range of chromosome numbers is found in plants that are very similar morphologically and that seem best regarded as all the same species. Thus construed, some species have four or more levels of polyploidy in different populations and many, perhaps most, widespread species have dysploid chromosome races (Uhl, 1972, 1978, 1980, and unpub.). For example, different populations of *Sedum wrightii* have five different levels of ploidy, $n = 12, 24, 36, 48,$ and 60 (Uhl, 1972, and unpub.). On the other hand, the wide-ranging *S. jaliscanum* has at least eight different dysploid chromosome numbers, ranging from $n = 11$ to $n = 34$ (Uhl, 1976), and Clausen (1981)

would also include plants having $n = 9$ and $n = 10$ as subspecies *angustifolium* of this species. The size of the chromosomes in *S. jaliscanum* varies inversely with their number, and it seems likely that the diversity of its chromosome numbers has resulted from rearrangements of chromosome parts on a massive scale, and that polyploidy is not present.

Sedum moranense HBK is a relatively small "typical" representative of the genus (chamaephyte), with white flowers and small, ovate to lanceolate leaves that are 2–4 mm long and almost as thick as wide, closely set in five or six spiral ranks (Clausen, 1959). Clausen also reported that plants from six populations were "remarkably similar morphologically", although environmental conditions, both in nature and cultivation, can significantly affect such characters as leaf size. One other population, subspecies *grandiflorum* Clausen, had larger flowers.

Sedum moranense is one of the commonest and widest ranging species of the Crassulaceae in Mexico. It occurs as disjunct populations, most often on volcanic rock above 2,000 meters, from the southern Sierra Madre Oriental in the states of Hidalgo, Puebla, and Veracruz west to the vicinity of Mexico City and Toluca and northwest to the Sierra de Guanajuato and to the interior mountains of San Luis Potosi; it is especially common in the state of Hidalgo (Fig. 1). The species also is common in cultivation in Mexico, and the collection reported here from Jalisco may have been introduced there.

This paper presents the chromosome numbers of 51 collections of *Sedum moranense* from 45 populations in all parts of its range (Fig. 1). Collections are listed in Table 1 in order of increasing chromosome number and then approximately from west to east and from north to south. At least 18 different chromosome numbers, from $n = 21$ (Fig. 2) to $n = 153$ (Fig. 17) have been found in the species, including apparent 5-, 7-, and 9-ploids but not counting variants with one or a few extra univalents or B-chromosomes. These represent apparent diploids, polyploids of probably nine different levels, and dysploids at several levels of ploidy.

Many collections have meiotic irregularities in the form of one or more unpaired chromosomes of standard size at metaphase I and laggards at anaphase I. Most univalents are easily identified by their conspicuously shallower depth in focus than bivalents and multi-

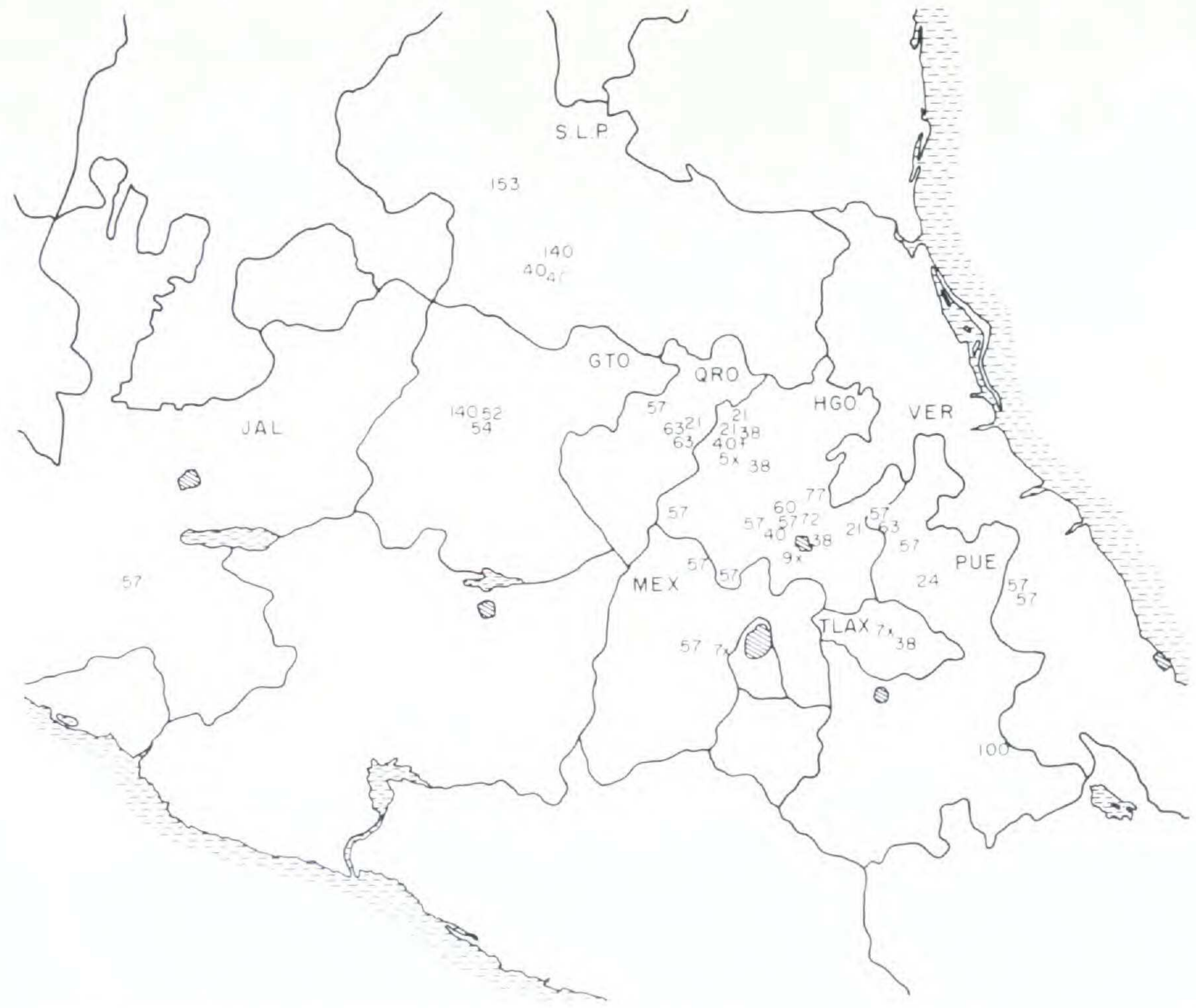


Figure 1. Central Mexico, showing locations of plants with various gametic chromosome numbers.

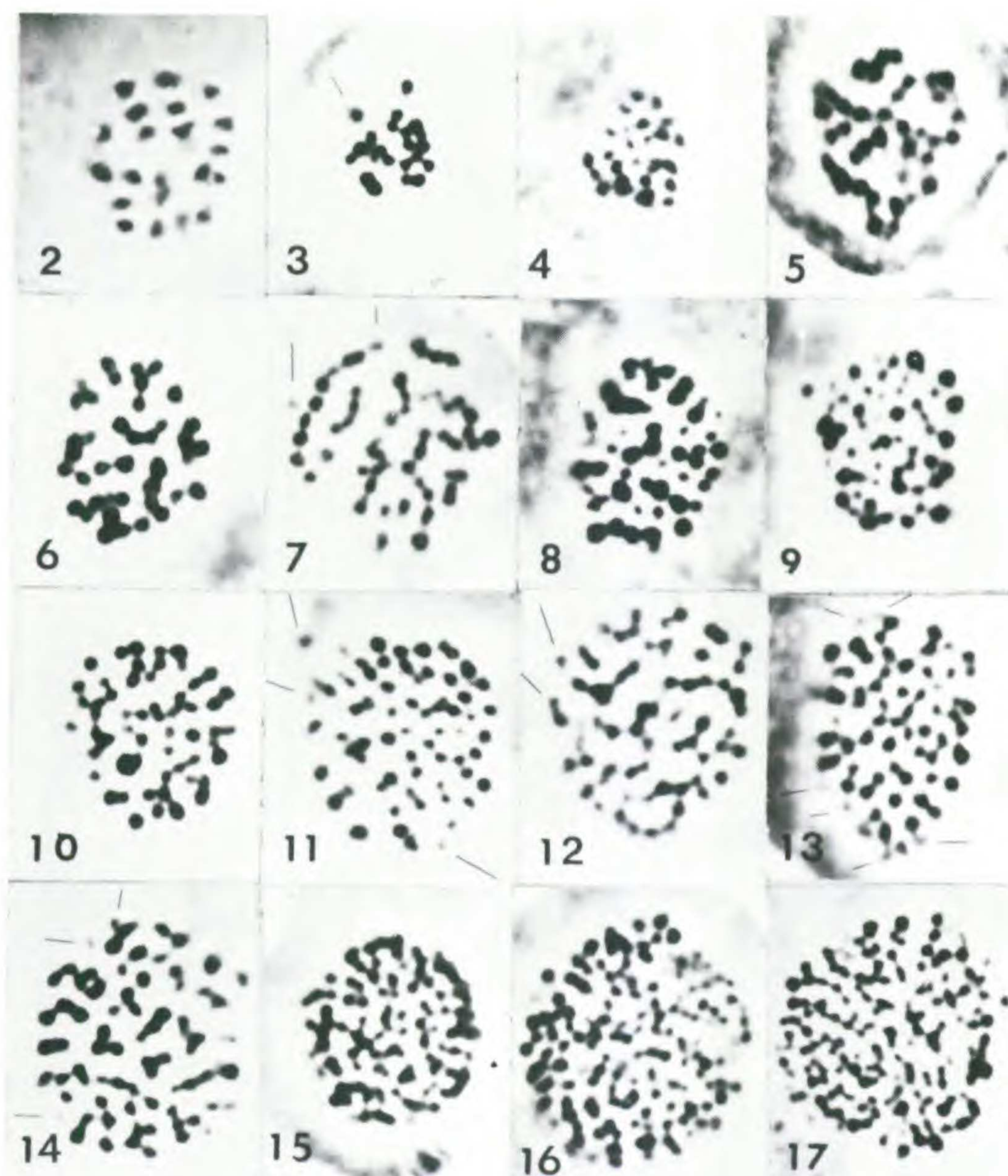


Fig. 2-17. Chromosomes of *Sedum moranense* at metaphase I, all $\times 2000$. Thin lines in some figures indicate univalents or B-chromosomes. 2, U1557, $n = 21$; 3, U1871, $n = 21 + 1$; 4, U2353, $n = 24$; 5, M13396, $n = 38$; 6, M7654, $n = 40$; 7, C44-109, $n = 50 + 2B$; 8, M14736, $n = 52$; 9, M10197, $n = 54$; 10, U2069, $n = 57$; 11, U830, $n = 60 + 3$; 12, U2128, $n = 62 + 2$; 13, 8d, $n = 63 + 6$; 14, M6414, $n = 77 + 3$; 15, U2487, $n = 100$; 16, M14734, $n = 140$; 17, U1536, $n = 153$.

valents and by their strong tendency to lie at the margins or sometimes off the plate at metaphase I. In one diploid (*U1871*, $n = 21 + 1$, Fig. 3) the unpaired chromosome is the largest present; at pachytene a heterochromatic body of about the same size is attached to the nucleolus. Very small extra, unpaired chromosomes, apparently B-chromosomes, are present in at least six collections. One diploid from Hidalgo (*U1870*, $n = 21 + 1$), two probable heptaploids from Tlaxcala (*7d* and *8d*), and one presumed octoploid from Hidalgo (*U2707*, $n = 72 \pm 1$) showed one or more chromosome bridges (up to 4) in most cells at anaphase I, presumably indicating heterozygosity for paracentric inversions.

The basic or ancestral chromosome number in *Sedum moranense* appears to be in the range of 18 to 21. Most polyploids have multiples of one or another of these numbers, up to 14-ploids with $n = 140$ in subspecies *grandiflorum* Clausen (Fig. 16) and a presumed 16-ploid (*U1536*) with $n = 153$ or very close to that (Fig. 17). Some multivalent associations are present in most cells of polyploids, and these make exact counts difficult (e.g., Fig. 10-17). Counts of plants having multivalents are reported here in terms of their equivalents as bivalents and are believed to be accurate within 2% at all levels of ploidy.

In each polyploid most cells at metaphase I generally produce a fairly constant number of bivalents, or their equivalents when multivalents are allowed for. However, especially in many of the higher polyploids, additional univalents of standard size are common at metaphase I. The number of these univalents is not constant in the cells of the same anther, which probably means that the extra chromosomes sometimes participate in forming multivalents and therefore that they are extra representatives of standard chromosomes of the genome. The species seems to be remarkably tolerant of chromosomal variation and unbalanced genetic dosages, especially at the polyploid level. Doubtless this tolerance has made possible the great variation that is found in the chromosomes of different populations.

One collection from Hidalgo (*U2343*) regularly had 40 paired elements (bivalents and multivalents) but also had 5-11 univalents of standard size and may represent a pentaploid based on $x = 20$. Two plants from the same population in Tlaxcala (*7d* and *8d*) had 60-62 paired elements plus 5-9 univalents (Fig. 13), and a plant from just

Table 1. Collections Studied.

<i>n</i> = 21	<i>U2129</i> Qro. 1 km. W. of San Joaquin, 2360 m. <i>U1870</i> Hgo. E. of Cuesta Colorada, 13 km. N. of Jacala, 1700 m. (<i>n</i> = 21 + 1) <i>U1871</i> Hgo. 1 km. N. of Minas Viejas, 2000 m. (<i>n</i> = 21 + 1) <i>U1950</i> Hgo. 1 km. S. of Minas Viejas, 2040 m. <i>U1557</i> Hgo. 11 km. E. of Tulancingo
<i>n</i> = 24	<i>U2353</i> Pue. 10 km. SW of Aquixtla, 2750 m.
<i>n</i> = 38	<i>U2708</i> Hgo. Ca. 1 km. N. of El Salto, km. 253 (<i>R. T. Clausen CMP-ES</i>) <i>M13396</i> Hgo. Near summit of mountain SE of Santuario, 2560 m. (R. Moran and C.H. Uhl) <i>C47-43</i> Hgo. Ca. 20 km. E. of Pachuca, 2320 m. (E.J. Alexander, via R.T. Clausen) <i>C47-38</i> Tlax. Barranca near San Bernabe Amaxac de Guerrerro (Ibid.)
<i>n</i> = 40	<i>M7654</i> SLP. Zaragoza (R. Moran) <i>U2705</i> SLP. 5 km. NW of La Salitrera (<i>R. T. Clausen 77-40</i>) <i>M7809</i> Hgo. San Vicente, ca. 3 km. S. of Durango (R. Moran) (<i>n</i> = 40 + 3B) <i>M7781</i> Hgo. Pachuca (R. Moran) (<i>n</i> = 40 + 1 + 5B) <i>U618</i> , <i>UC44-110</i> Cultivated
Probable pentaploid	<i>U2343</i> Hgo. 4.3 km. S. of Durango, 2130 m. (<i>n</i> = 40 + 5-11)
<i>n</i> = 50	<i>FL1419</i> Cultivated (<i>n</i> = 50 + 1B) <i>C44-109</i> Cultivated (<i>n</i> = 50 + 2B)
<i>n</i> = 52	<i>M14736</i> Gto. Santa Rosa, 2590 m. (R. Moran) <i>U2288</i> Gto. 3 km. SW of Mesa San Jose and 22 km. NE of Guanajuato, 2360 m.
<i>n</i> = 54	<i>U2267</i> Gto. 10 km. NE of Guanajuato, 2560 m. <i>M10197</i> Gto. Near Santa Rosa (R. Moran) (<i>n</i> = 54 + 1B)
<i>n</i> = 57	<i>U2069</i> Jal. SW edge of Tapalpa, 2130 m. (F. C. Boutin & M. Kimnach) <i>U1952</i> Qro. 5 km. S. of Pinal de Amoles, 2560 m. <i>U1854</i> Qro. 8.5 km. S. of Pinal de Amoles, 2600 m. <i>U1476</i> Hgo. Presa Madero, 12 km. W. of Huichapan <i>U1484</i> , <i>U1485</i> } Edo. Mex. 10.5 km. WNW of Soyaniquilpan (N.W. Uhl & W. Handlos) <i>U1481</i> Hgo. 7.5 km. SE. of Tepeji del Rio (N.W. Uhl & W. Handlos) <i>U1877</i> Hgo. 2 km. S. of Tepenene <i>U1466</i> Hgo. Near Pueblo Nuevo <i>C47-44</i> Pue. Near Honey. (H. Xolocotzi, via E. J. Alexander & R. T. Clausen) <i>U1554</i> Pue. 22 km. NW of Zacatlan <i>U1418</i> Edo. Mex. Hill N. of Toluca, 2740 m. <i>6d</i> Ver. Near Las Vigas (R. T. Clausen) (<i>n</i> = 57 + 3) <i>U1884</i> Ver. 27 km. NW of Jalapa, 2290 m.

- $n = 60$ *U830* Hgo. El Chico, 3000 m. (H. E. Moore) ($n = 60 + 2$)
- $n = 63$ *U2128* Qro. 13 km. W. of San Joaquin, 2330 m. ($n = 63 + 1$)
U1556 Pue. Puente Totolapa, 11 km. W. of Huauchinango
U2706 Edo. Mex. El Zarco, Sierra de las Cruces (R. T. Clausen 55-169)
- Probable *7d, 8d* Tlax. Atlihuitzia (R. T. Clausen) ($n = 60-62 + 5-9$)
heptaploids.
- $n = 72$ *U2707* Hgo. Cerro Jardin, W. slope, 2480 m. (R. T. Clausen 76-47)
- $n = 77$ *M6414* Hgo. Canon Venados (R. Moran) ($n = 77 + 3$)
- Probable *U1548* Hgo. 2 km. S. of Epazoyucan ($n = 80 + 10$)
9-ploid
- $n = 100$ *U2487* Pue. 1 km. W. of Nicolas Bravo, 2600 m. (one clump only)
- $n = 140$ *10d* SLP. Mountains (Sierra de Alvarez) E. of San Luis Potosi (R. T. Clausen) Clonotype of *S. moranense* ssp. *grandiflorum*
U1641 SLP. 2 km. W. of highway summit, Sierra de Alvarez, 2260 m. (W. Handlos)
M14734 Gto. Picachos de la Bufa, cliffs NE of Guanajuato, 2290 m. (R. Moran)
- $n = 153$ *U1536* SLP. 16 km. N. of Ahualulco

west of Mexico City (*U2706*) formed about 57 paired elements and 5-8 univalents; these three are believed to be heptaploids based on $x = 19-21$. Another plant from Hidalgo (*U1548*) had probably 80 paired elements plus about 10 univalents and is thought to be 9-ploid. Presumably the number of chromosomes of the last (odd) set that participate in the formation of multivalents is variable, which leaves a variable number of them as univalents in different cells.

In most plants the bivalent chromosomes at metaphase I do not differ greatly among themselves in size (Fig. 2, 5, 6, etc.), and any extra univalents that may be present also appear to be of the same size. However, four collections from the Sierra de Guanajuato differed strikingly from nearly all other collections in having a wide range of sizes among their 52-54 bivalents at metaphase I (Fig. 8, 9). This condition (heterogeneous or asymmetrical karyotype) is generally believed to have been derived by unequal translocations from ancestors having chromosomes more nearly equal in size (homogeneous or symmetrical karyotype) (Stebbins, 1971). The numerically anomalous diploid from Puebla (*U2353*, $n = 24$) also has bivalents that differ more than usual in size (Fig. 4), although not as much as they do in the plants from Guanajuato. Two collections with $n = 50$, both of unknown provenance from the wild, have

bivalents that are more or less equal in size, although their 1 or 2 extra chromosomes are tiny and interpreted as B-chromosomes (Fig. 7).

With so many chromosome races and so many levels of ploidy, some of them occurring close to each other, it is probable that considerable intercrossing has occurred between plants having different chromosome numbers and that such intercrossing has been a source of still more cytological variation. The evident viability and tolerance of unbalanced chromosome dosages would make survival possible until new, more or less stable chromosome complements evolved. However, the phenotypic effects of this sort of variation, including some apparent cases of unbalanced dosages of chromosomes, appear to be negligible. The effects, if any, on fertility or adaptation to the particular habitat are not clear. It is possible that some apomixis occurs here, but as yet there is no direct evidence for it. Qualitative and quantitative chemotaxonomic studies on these plants might prove interesting.

According to Clausen (1959) *Sedum liebmannianum* of the Sierra Madre del Sur is the species most closely related to *S. moranense*, but it differs conspicuously in its persistent, withered leaf bases. Two collections of *S. liebmannianum* had $n = 34$, but seven other collections were very irregular at meiosis and probably odd-ploid. A similar plant from Puebla with smaller leaves (U2358) had $n = 30$. Clausen (1959) also cited two other species as related to *S. moranense*: *S. cupressoides* ($n = 29$) of the Sierra Madre del Sur and *S. parvum* ($n = 32, 34, 64$) of northeastern Mexico, to which he later (1978) also reduced *S. nanifolium* ($n = 26, 52$). Chromosome numbers of these species (all from Uhl, unpublished) do not support any conclusion that they are closely related to *S. moranense*.

Clausen (1959) studied a plant said to have come from high on the Nevado de Toluca that he thought might be a hybrid between *Sedum moranense* and *Villadia batesii*. The plant is intermediate in morphology and produces abortive pollen and ovules. Eight cells at metaphase I had 24 to 27 bivalents and multivalents plus 3 to 14 univalents, and the microspores after meiosis differ among themselves in size and stainability. Nineteen collections of *V. batesii* from Puebla and Hidalgo to Michoacan, including one from the Nevado de Toluca, all had $n = 25$, which is considered to represent a diploid here (Uhl, unpublished). However, no collection of *S. moranense*

from the Nevado de Toluca has been studied, and Clausen (1959) does not cite this as a locality for the species. The nearest *S. moranense* that has been studied came from just north of the city of Toluca, about 24 km. north of the volcano, and had $n = 57$, considered hexaploid. Clausen's plant appears clearly to be a hybrid, but its chromosomes and its location make it very doubtful that *S. moranense* could have been one of its parents.

Clausen (1981) suggested that *Sedum furfuraceum* ($n = 34$, Uhl, 1980), which is known from only one population in San Luis Potosi, might have originated at that site as a hybrid between *Pachyphytum hookeri* and *S. moranense*, both of which occur with it there. However, *S. moranense* there (M7654) is tetraploid ($n = 40$), and *P. hookeri* there is decaploid ($n = \text{ca. } 160$, Uhl and Moran, 1973), and this suggested relationship seems most unlikely.

Many hundreds of hybrids have been produced in cultivation within and between *Sedum* and various other Mexican genera. However, only one cross has been attempted with *S. moranense*; U1642 (*S. retusum*, $n = 27$, Uhl, 1980) \times U1557 (*S. moranense*, $n = 21$), and this was unsuccessful. Analysis of chromosome pairing in hybrids of *S. moranense* having different chromosome numbers could allow their levels of ploidy to be identified, as has been done with *Echeveria* (Uhl, 1982ab).

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